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The Genetics and Evolution of Female Choice

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Darwin based his theory of evolution on the central theme of 'the struggle for existence', 'the preservation of favoured races', 'the survival of the fittest'[1]. *In addition to this 'natural selection', he proposed a second type of selection, sexual selection. 'This depends, not on a struggle for existence, but on a struggle between males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring'*[1]. *Males would compete for females, and females would choose between males. Since Darwin's work, many examples of natural selection have been observed in nature and in laboratory experiments, and knowledge of genetics has given natural selective theory a sound basis. The theory of sexual selection through male competition has also been widely accepted. However, the theory of sexual selection through female choice has had a much more chequered passage.*

Critics of the theory of sexual selection by female choice argued that since female choice was used to explain elaborate secondary sexual characteristics in males[1,2], Darwin was implicitly postulating the presence of a highly developed aesthetic sense in the females[3–5]. Female choice was also criticised because Darwin did not suggest a pathway for the evolution of mating preferences, but rather took their existence as a premise to explain male ornaments[4].

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Fisher's theory of sexual selection by female choice

A mechanism for the evolution of female choice was eventually proposed by Fisher[6], who suggested that a novel genetic male character, spreading through a population as a consequence of a slight natural selective advantage, might become the object of a genetically determined female mating preference. Females exercising the preference produce fitter progeny because they have paired with males that have a genetically controlled natural selective advantage. Those males which possess the trait picked out by the choosy females will now gain a reproductive advantage, because they will be more likely to pair than males lacking the preferred character; this is in addition to the natural selective advantage of males with the preferred character. Consequently, the female preference and the preferred character each increases the advantage which accrues to the other, so that they advance together. Unless checked by some other counter selection the rate of in-step coevolution will increase geometrically, giving rise to what Fisher called the 'runaway process of sexual selection'[6].

Genetical models of female choice

Uncharacteristically, Fisher did not put the theory of sexual selection onto a framework of Mendelian genetics as he had done with natural selection. The continued lack of support for female choice[4,5,7–9] may be partly attributed to this omission. However, O'Donald[10–12], Lande[13] and Kirkpatrick[14] have subsequently formulated genetical models of Fisher's theory. In O'Donald's models, a diploid organism has preferences control-

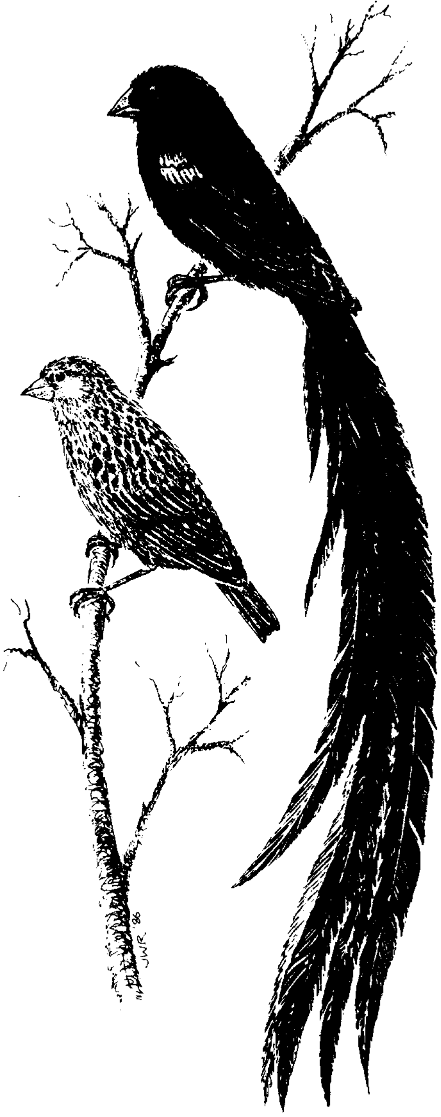

Fig. 1. The widowbird, *Euplectes progne*. Females prefer males with longer tails.

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Trends in Ecology and Evolution

The number of regular publications dealing with ecological, environmental and evolutionary research has increased remarkably over the past two decades, fuelled by the growth of universities and research institutes worldwide, by the birth and development of major new subdisciplines and by the awareness of the many threats to natural and managed ecosystems that arise from human activities. A glance through the regular accessions of any good biological library will reveal more than fifty periodicals directly relating to ecological or evolutionary themes, and many more that cover associated subjects.

Despite the current cutbacks in funding for research, new journals continue to appear, making the task of keeping up with new developments ever more difficult. Oddly enough, this is precisely why *Trends in Ecology and Evolution* is necessary. Every month this new journal will furnish short, up-to-date reviews, commentaries and news items about all areas of ecological and evolutionary research, with the intention of channeling and distilling the flow of new ideas and information into a form that is accessible to specialists from all subdisciplines.

We also aim to reflect and encourage the increasing cross-fertilization between subdisciplines, and to break down some of the artificial barriers that have arisen with the diversification of ecological and evolutionary studies. The 'pure' will be mingled with the 'applied', the terrestrial with the marine, and the botanical with the zoological. No quota will be set for the amount of space to be allotted to particular areas of research; topics will be covered on the basis of current interest and promise. Readers should not expect to find the full range of topics (or, indeed, their own particular field) featured in every issue of *Trends in Ecology and Evolution*, but they will always find out what is exercising the minds of their colleagues.

A further goal deserves mention. *Trends in Ecology and Evolution* is published in English, but it is not intended as a service or mouthpiece for scientists from anglophone countries alone. Although ecological and evolutionary thought had its roots in these countries and in continental Europe, a great deal of practical effort is now concentrated elsewhere. We hope to provide representative cover of current research in all regions, reflecting the international nature of the science.

The titles of the articles in this issue and of those scheduled for the forthcoming months (listed on this page) give an indication of how we intend to fulfil these aims. Much work remains to be done, nevertheless, and we shall therefore welcome suggestions from readers on ways in which *Trends in Ecology and Evolution* might be developed and improved. The journal will be successful only if the interests of the audience are taken into account.

Readers of *Trends in Ecology and Evolution* will not be subjected to regular contributions from the Editor. I would therefore like to take this opportunity to thank all those whose assistance and hard work has enabled us to get off to a good start, especially the members of the Advisory Editorial Board, our authors, and the staff at Elsevier's Cambridge office (home of the other biological *Todays Trends* journals). Thanks are also due to all those prospective readers whose enthusiasm and constructive ideas have helped *Trends in Ecology and Evolution* towards a successful launch.

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led by alleles at one locus, the preferred phenotypes being determined by alleles at another locus. The rate of increase for the preference is initially geometric, but then rapidly slows down, contrary to Fisher's conclusion. Recessive alleles are generally selected more rapidly than dominants. In Lande's model, preference and preferred character are both controlled polygenically. They are assumed to be normally distributed and determined by an indefinitely large number of genes, each with minor effects. The result is that selection for preference is proportional to the selection for the preferred character, so the rate of increase for the preference is geometric. Both preference and preferred character continue to increase without limit. Of course, this is biologically unrealistic. Any limitation in the number of loci which actually determine the females' preference will place genetic limits on the final level attainable by both preference and preferred character. Kirkpatrick's model is similar to those of O'Donald in that preference and preferred character are each controlled by single loci; however, he works with a haploid system. The analytical results are qualitatively similar to those from O'Donald's models.

These models confirm that the in-step coevolution of preference and preferred character is plausible. However, an initial advantage to the male trait is not essential, and the rate of evolution is not necessarily geometric. It depends critically on the genetic basis of both the preferred character and the preference, as well as on the behavioural expression of the preferences, and the initial frequencies of the preferred traits and preferences.

Experimental evidence that females choose between males

The lack of support for female choice theory has been exacerbated by a lack of direct evidence that females do choose between genetically different males. Such evidence has been slow in accumulating, partly because the two mechanisms of sexual selection, male competition and female choice, can only be distinguished by carefully controlled experiments. For instance, female three spine sticklebacks (*Gasterostens aculeatus*) prefer to lay their eggs in the nests of red-throated males when given a choice between these and non-red males[15]. But are they choosing the red-throated males, or are these males simply more active or aggressive when courting females? Semler distinguished between these two alternative explanations by first showing that females prefer red males to non-reds[15]. He then offered females a choice between two genetically non-red males, one of which had been artificially given a red throat with lipstick or nail varnish. Again the 'red-throated' males were more successful. Since the artificially red males were genetically the same as the non-red males, the red males' success must have been the result of females having a preference for these males.

The sexual selection/natural selection balance

If females prefer red males, why do not all male sticklebacks have red throats? In fact, in some populations all males are red-throated, but in others males are polymorphic. It seems that there is a cost to red-throatedness which acts against the reproductive advantage accruing to red-throated males. In Lake Wapato there is intensive predation of sticklebacks by rainbow trout which strike differentially at red males over non-reds when both are present[16]. A balance between sexual and viability selection may thus be reached. The maintenance of the polymorphism is facilitated because the reproductive advantage of the red males is frequency-dependent. If a constant proportion of females prefer red-throated males, then as several females may lay eggs in a single male's nest, preferred males will gain a greater advantage when they are rare than when they are common.

Fisher[6] suggested that sexual selection by female choice is directional. A male character which has become the object of a female mating preference would continue to increase in development until any further increase was checked by counter natural selection. As O'Donald[17] has pointed out, this will only apply if females have a preference for males with a more than average development of the character. The male character is then acting as a supernormal stimulus to the females. The outcome of such a system should be that female preferences for greater than average development of a character will be precisely balanced by the natural selective disadvantage of any greater development.

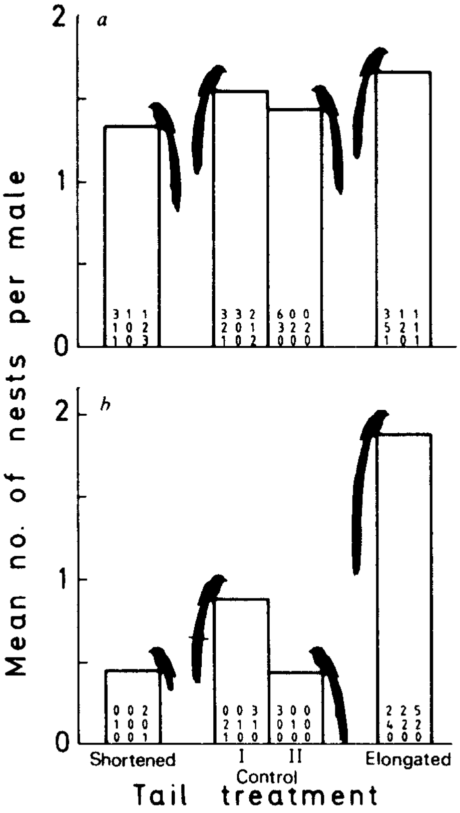

Fig. 2. Mating success in male long-tailed widows subjected to different tail treatments. (a) mean number of active nests per territory for the nine males of the four treatment categories, before the experiment. Number of nests for the nine males in each of the four categories are given at the bottom of the bars, always in the same order of matched 4-group. (b) number of new active nests in each territory after treatment of males. With permission from *Nature*.

Perhaps the most dramatic illustration that females may indeed have a preference for increased development of a secondary sexual character comes from Andersson's elegant work on the long-tailed widowbird *Euplectes progne*[18]. In this species females are mottled brown with short tails. Males are black with a red epaulet on the wings, and have very long tails (Fig. 1) which are extremely conspicuous when the males are in flight over breeding territories. Andersson changed the tail lengths of male birds by cutting the tail feathers of some, and using the cut off sections to extend the tail lengths of others.

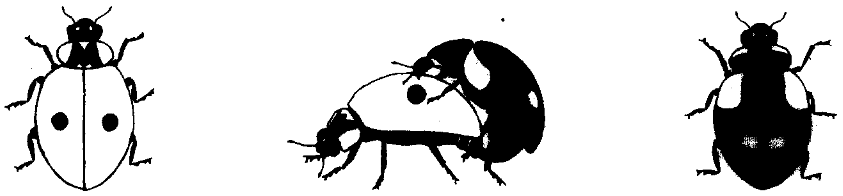

Fig. 3. Melanic and non-melanic forms of the two-spot ladybird, *Adalia bipunctata*. A melanic male is shown mating with a non-melanic female.

Two control groups were also used. In one the tails were cut, and then restored to normal length. In the second the birds were simply captured and released. Andersson then recorded the number of nests made by females in the territories of nine males from each of these groups. The results (Fig. 2) demonstrate that the males with lengthened tails had greatest success, and those with shortened tails had least. These data corroborate the Darwin–Fisher theory of sexual selection. Females preferred males having longer than normal tails as expected if the preference of the females is expressed as a response to a supernormal stimulus.

Increased reproductive success due to mate choice

It is essential to models of preferential mating that the expression of preferences by one sex can confer increased reproductive success on individuals of the other sex which possess the preferred character. In the sexually dimorphic zebra finch *Poephila guttata* individuals of both sexes prefer opposite sex adults with plastic leg bands of certain colours, and avoid those wearing other colours[19]. When males were randomly assigned bands of red ('attractive to females'), or green ('unattractive') or orange ('neutral') and tested with unbanded females, the red-banded males achieved approximately twice the reproductive success of other types. Similarly, when females, which were randomly assigned black ('attractive to males'), or blue ('unattractive'), or orange ('neutral') bands, were tested with unbanded males, the black-banded females produced twice as many offspring as blue-banded females. Females of intermediate attractiveness had intermediate reproductive success[19].

That female choice can also increase the reproductive success of females exercising a preference has been demonstrated by Ryan[20]. He showed that females of the tungara frog *Physalaemus pustulosus* choose larger than average males as mates. The male mating call in this species consists of one 'whine' and from 0–6 'chucks'[21]. There is a significant negative correlation between male size and the fundamental frequency of the chuck. The ability of females to discriminate between larger and smaller males depends on the frequency of the chuck. Ryan also demonstrated that females that choose larger males have an increased reproductive output.

The rare male effects

In some cases it has been suggested that females do not have a preference for a particular male genotype, but rather that they have a preference for males of rare genotypes. These 'rare male effects' have been sought most often in *Drosophila*. For example, Spiess and Spiess[22] demonstrated a rare male advantage when females were offered a choice of males homozygous for one or other of two inversions. They explained the results by suggesting that females become habituated to the display of common males, and so are more likely to mate with an unusual male because the state of habituation is broken. However, O'Donald[23] showed that the data were also consistent with a model of constant preferences, females having a preference for one or other of the male phenotypes. The frequency dependence in the males' mating advantage is a necessary consequence of the expression of constant female preference.

The rare male effect may thus be a product of the females' avoidance of common courtship types or purely a manifestation of the frequency dependence inherent in preferential mating systems of this type. This controversy appeared to be resolved by Spiess and Kruckeberg[24]. Using red- and orange-eyed flies they showed that females avoided mating with males of the type which first courted them.

Table I. Numbers of non-melanic (*typica*) and melanic (*quadrimaculata*) two-spot ladybirds in population cages in successive generations and estimates of female preference[27].

Generation	Total number in cage		Number of matings between different phenotypes				Estimates of preference for Q
	N_T	N_Q	QxQ	QxT	TxQ	TxT	$\hat{\gamma} \pm \sqrt{var}$ ($\hat{\gamma}$)
Selected line							
1	224	96	21	31	24	46	0.1803 ± 0.0640
2	112	48	13	18	9	14	0.3915 ± 0.0961
3	84	36	12	14	6	10	0.4558 ± 0.1070
4	140	60	18	21	5	12	0.5663 ± 0.8780
Control line							
1	98	42	13	15	8	21	0.2732 ± 0.0946
2	70	30	7	11	7	12	0.2664 ± 0.1174
3	112	48	10	18	10	18	0.2857 ± 0.0955
4	112	48	11	22	13	28	0.2085 ± 0.0825

Analysis of χ^2

Component of variation	Values of χ^2	d.fs	Values of P
Between selected and unselected groups	12.5103	1	0.000405
Within selected populations	1.6837	2	0.431
Within unselected populations	1.3000	4	0.861

N_T and N_Q refer to the total number of *typica* (T) and *quadrimaculata* (Q) ladybirds of a given generation that were placed in a population cage for mating. They consisted of equal numbers of males and females. The male phenotype is shown first in the type of mating: Q×T is a mating of Q♂ × T♀; T×Q is a mating of T♂ × Q♀. The males were replaced in the cage after they had mated. The preferred males often mated more than once during the 5 or 6 days of observation of a cage. Females were not replaced after mating. If observations had been continued until all females had mated, an exact 7:3 ratio of T:Q females would necessarily have been found to have mated. However, after 6 days, 90% of Q and 60% of T females had mated. Comparing numbers of mated and unmated females among Q and T females in the selected line, we obtain $\chi^2_3 = 1.4962$, showing no change in mating propensities of Q and T females with increasing preference over generations. The Q and T females show similar levels of preference, but the T females are slower to mate. 'd.fs' in the analysis of χ^2 means the numbers of degrees of freedom.

Table 2. Mating tests between the selected line and original Keele stock[27].

Numbers of matings and estimates of preferences

Stocks and sexes used in matings	Numbers of matings between different phenotypes				Estimates of preference for Q
	Q×Q	Q×T	T×Q	T×T	$\hat{\gamma} \pm \sqrt{\text{var}}\ (\hat{\gamma})$
Selected ♂♂ × Keele ♀♀	11	28	17	34	0.1905 ± 0.0746
Selected ♀♀ × Keele ♂♂	16	28	6	15	0.5385 ± 0.0829
Keele ♂♂ × Keele ♀♀	18	35	21	42	0.2241 ± 0.0661

Analysis of χ^2

Component of variation	Value of χ^2	d.fs	Value of P
Selected males compared with Keele males	0.1126	1	0.737
Selected females compared with Keele females	10.4844	1	0.00120

The selected males and females used in these tests were taken from the progeny of the fourth generation of the selected line. No further selection had been imposed after the fourth generation. The level of preference among the progeny of the fourth generation should be the same as that in the fourth generation. The selected males and females were tested in matings with progeny taken from the corresponding generation of the original Keele stock. Population cages were set up with 7:3 ratios of T:Q. They were kept under continuous observation; mating pairs were counted giving the numbers shown in the table.

However, these results have been challenged by Partridge and Gardner[25] who have been unable to replicate Spiess and Kruckeberg's results despite using similarly constituted stocks.

It is worth pointing out that a general female preference for the rarest male is difficult to comprehend on evolutionary grounds, because any new mutation, whether advantageous or disadvantageous, would immediately gain a mating advantage.

The genetics of female choice

A comparison of the various theoretical models of Fisher's theory of the evolution of sexual selection by female choice shows that the exact genetic control of female preferences has important consequences for the evolutionary process[12–14]. That female mating preference may be inherited has recently been demonstrated in the two spot ladybird, *Adalia bipunctata*. This species is polymorphic for melanic and non-melanic forms (Fig. 3). Majerus *et al.*[26] showed that there was an excess of melanic males in matings with both melanic and non-melanic females. The excess of melanic males in mating pairs could be increased by artificial selection. By selecting only those females that had mated with melanic males to produce each subsequent generation, the level of preference for melanic males was increased from 20% to 50% in three generations[27] (Table 1). These results suggest that the sexual selection has a genetic basis. That the excess of melanic males was due to female choice and not male competition was demonstrated formally using this high preference stock[27] (Table 2). When the level of preference was tested using males from the high preference line with females from the unselected Keele population, the level of preference was characteristic of the level in the original population. However, when females from the high line were tested with males from the original Keele population, the level of preference was characteristic of the high selected line.

Subsequently, the selection experiment has been repeated and extended[28]. Lines selected for both increased and reduced preference have been produced. Over eight generations of selection, the level of preference in the high line was raised to 65%. In the line in which selection was imposed against female preference for melanic males, the level of preference dropped rapidly to zero. However, no female preference for non-melanic females was achieved.

At generation 10, single pairs were selected at random from the high line. Large numbers of progeny were reared from these pairs to allow measurement of the female preference within each isofemale line. The results (Table 3) showed great variation in the level of preference, but with substantial gaps in the distribution. The isofemale

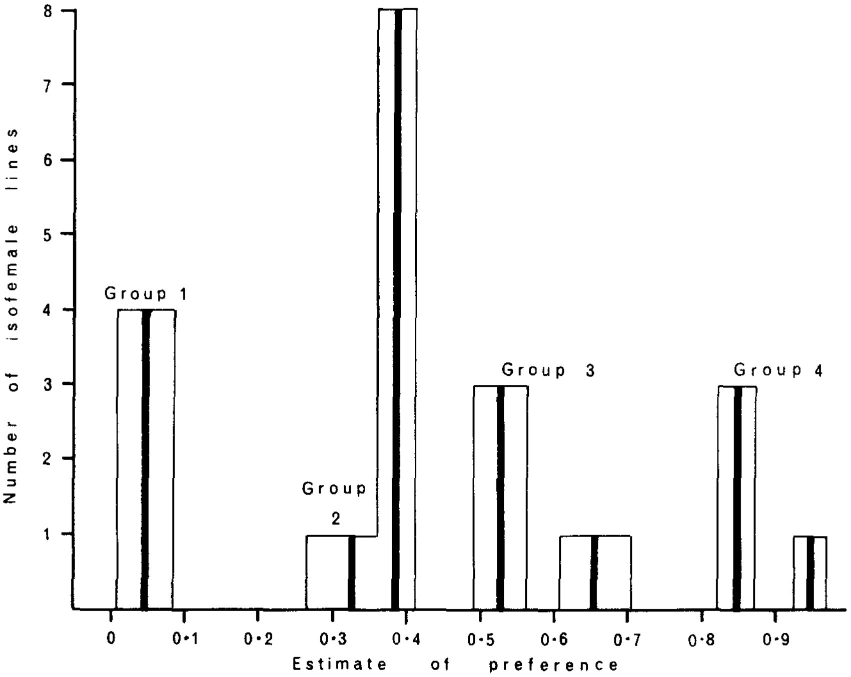

Fig. 4. Isofemale lines shown divided into four distinct groups. The solid black bar shows the position of the estimated preference in the given number of lines; open bars, the standard error. In groups 2, 3 and 4 the preference is also shown for the line most divergent from the others in the group. When groups are considered separately, each of groups 1, 2 and 3 is found to be statistically homogeneous. Group 4 is heterogeneous, with line Z35 having a significantly higher preference. In later population cage experiments, however, Z35 did not show a higher preference. The total χ^2 for heterogeneity within all groups is not significant (Table 3). With permission from *Nature*.

Table 3. Results of formal mating tests on mating preferences in isofemale lines of the two-spot ladybird[29].

(i) Frequencies of matings with males

	Isofemale Line	Mated males Q	Mated males T	Total males Q	Total males T	Estimate of preference $\hat{\gamma}\pm\sqrt{\text{var}}\ (\hat{\gamma})$
Group 1	Z4	51	48	210	210	0.033 ± 0.088
	Y4	218	204	815	815	0.038 ± 0.042
	Z33	49	45	220	220	0.046 ± 0.091
	Y12	57	52	245	245	0.050 ± 0.084
	Totals	375	349	1490	1490	0.041 ± 0.032
Group 2	Y18	134	73	395	395	0.324 ± 0.055
	Y14	149	74	435	435	0.367 ± 0.052
	Z36	141	69	400	400	0.375 ± 0.053
	Y13	223	107	700	700	0.380 ± 0.043
	Z17	212	102	620	620	0.381 ± 0.044
	Z34	141	66	420	420	0.393 ± 0.054
	Z20	68	33	125	125	0.398 ± 0.067
	Y15	154	70	395	395	0.411 ± 0.049
	Z32	74	32	200	200	0.430 ± 0.072
	Totals	1296	626	3690	3690	0.381 ± 0.018
Group 3	Z13	218	79	590	590	0.501 ± 0.042
	Y9	150	50	360	360	0.537 ± 0.048
	Z16	80	26	200	200	0.544 ± 0.067
	Y3	153	36	335	335	0.654 ± 0.044
	Totals	601	191	1485	1485	0.553 ± 0.024
Group 4	Y19	272	34	575	575	0.801 ± 0.028
	Z37	91	6	240	240	0.887 ± 0.040
	Z40	102	5	200	200	0.918 ± 0.031
	Z35	203	7	385	385	0.942 ± 0.018
	Totals	668	52	1400	1400	0.872 ± 0.015

(ii) Analysis of χ^2

Component of variation	Degrees of freedom	Value of χ^2	Value of P
Between groups	3	362.39	–
Within groups	17	24.69	0.102
Within replicates of lines	19	20.35	0.374
Total	39	407.43	–

Isofemale lines were produced by randomly selecting pairs from the tenth generation of the selected line. The level of preference of progeny from these lines was estimated by offering females a choice of melanic (Q) or non-melanic (T) males at a 1:1 ratio.

In this analysis of χ^2, the data of replicates of tests on individual lines have not been included in the table. Totals over replicates within lines are shown. The analysis of χ^2 is based on the null hypothesis of random mating of male phenotypes: it is an analysis of the values of χ^2 for interaction in the $2 \times 2 \times N$ table of numbers of mated and unmated phenotypes of males in tests on the isofemale lines. Note that the same males and females may be used several times in successive series of tests.

lines could be divided into four groups on the basis of their preferences (Fig. 4). Such a division is consistent with the hypothesis that female preference for melanic males is controlled by a single dominant gene[29].

How widespread is female choice?

The female preference for melanic males in *Adalia bipunctata* is a true genetic polymorphism: some females have the preference allele, others do not. In the ladybirds, natural and sexual selection apparently act to maintain a genetic polymorphism of melanic and non-melanic forms[30,31]. In the most obvious and widely quoted examples in which female choice has been implicated (such as the breeding plumage of male peacocks, pheasants, ruffs and birds of paradise) the males alone show the highly developed and colourful characters for sexual display, while the females are often cryptic in colouration. The males may be polymorphic in their breeding colours like the ruff, or monomorphic like the peacock; the females are monomorphic. But although sexually selected, the ladybirds show no such sexual dimorphism: both sexes show the same polymorphism of melanic and non-melanic phenotypes. Thus, the theory of sexual selection by female choice may apply far more widely than has generally been supposed. It could explain not only the evolution of highly developed display characters in males, but also the maintenance and evolutionary stability of simple genetic polymorphisms in which no sexual dimorphism is present. Female choice has been implicated in the maintenance of other non-sex-limited polymorphisms in the scarlet tiger moth[32], the snow goose[33–35], the arctic skua[36], and even the polymorphism of electrophoretic allozymes in the milkweed beetle *Tetraopes tetraopthalamus*[37]. However, the genetic basis of the mating preference has not been demonstrated in any of these. The control of female choice by a simple genetic mechanism like a single dominant gene will allow for the appearance and rapid evolution of a frequency-dependent mechanism which can maintain such polymorphisms.

One is tempted to question whether such mating preferences could have still wider applications. If female mating preference implicated in the maintenance of traits which are not sex-limited it may not be necessary to confine mating preferences to females discriminating between males. Darwin[2] used female choice to explain sexual dimorphism, leaving plumage in sexually monomorphic birds to be explained by natural selection. However, the evolution of elaborate plumage in birds where the sexes differ little, such as great crested grebes, or crown cranes, could be seen as the outcome of genetically controlled mating preferences which are expressed in both sexes. Such preferences would reduce the possibility of hybridization between populations or species showing a degree of post-zygotic isolation manifested by the reduced viability or fertility of the hybrids. Sexual selection would be promoted because the avoidance of hybrid matings will be favoured. So, sexual selection through mating preferences could be a potent force in the evolution of pre-mating reproductive isolation mechanisms.

The finding that the choices made by female ladybirds are controlled by a single dominant gene may also be important in the context of the sociobiological interpretation of animal behaviour. Many sociobiological models have assumed that alternative behavioural strategies – for example whether to accept or reject a particular mate, or whether to be a 'hawk' or a 'dove' in conflicts – are simple genetic polymorphisms[38,39]. These simple models of complex behaviour have been challenged by some opponents of sociobiology[40]. Yet in *Adalia bipunctata* female choice behaviour is both genetic and polymorphic.

The theory of sexual selection by female choice now stands on firmer ground. The models of O'Donald, Lande and Kirkpatrick have shown that a mechanism for the evolution of female choice is plausible. Males with more elaborate secondary sexual characters may be more successful. Experiments have shown that females may choose between males, that males with more extreme elaborate secondary sexual characters may be more successful in attracting females than males with less extreme developments, that a female's preference for specific males may result in an increase in a female's reproductive success, and that female mating preferences may be genetically polymorphic.

At present, however, there is no known case in which the complete system of sexual selection through female choice has been uncovered. The two-spot ladybird is the only case in which the genetic basis of female mating preference has been analysed. However, although the selective factors which must act to balance the advantage which accrues to the melanic form due to female preferences for them have been quantified[30], the nature of these factors is unknown. Furthermore, the sensory cues used by female two-spot ladybirds to discriminate between different males are also unknown. If future work on the ladybirds can demonstrate how females choose between males, and the selective factors which act to balance the sexual selection, a population genetic model of sexual selection based for the first time on knowledge of the genetics of female mating preferences could be tested against observation. The genetic basis of female mating preferences must be analysed in other species in which female choice has been implicated, to discriminate between Lande's polygenic model of female choice and O'Donald's single gene models, and to provide the basis for more realistic appraisals of the importance of sexual selection by female choice.

Acknowledgements

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